47. Contributions to the Anatomy and Systematic Arrangement of the Cestoidea. By Frank E. Beddard, M.A., D.Sc., F.R.S., F.Z.S., Prosector to the Society.

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(Text-figures 1-11.)

XIV. On a new Species of Rhabdometra, and on the Paruterine Organ in Otiditænia.

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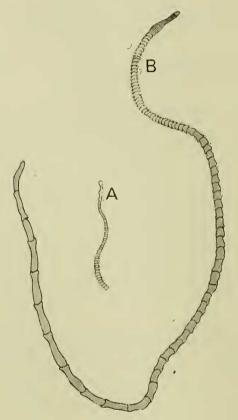
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I have recently obtained a considerable number of examples of a Tapeworm from an African Partridge, Caccabis melanocephala, which I refer, temporarily at least, to the genus Rhabdometra, though a closer comparison of this worm with the known species of Rhabdometra may ultimately necessitate its separation from that genus. The worm occurred in the Partridge associated with several other species, and I found always a relationship in numbers between the different forms which inhabited that bird. I examined altogether five specimens of the Caccabis in three of which were found examples of the Rhabdometra. In two examples there were a large number of specimens of the Rhabdometra, and in the other example only two specimens. The birds, which were infested by many specimens of Rhabdometra, contained also apparently only one representative of other species of Tapeworms. In the one case it was a Davainea and in the other a Cotugnia (?) In the bird where there were only two Rhabdometra there were many Davaineae.

The general appearance of this worm is indicated in text-fig. 1. It is long and slender; when alive the longest examples were fully six inches or so in length. In spirit the dimensions are somewhat lessened. This great length is accompanied by only a small diameter; the width varies from something under one millimetre, to a little over a millimetre. The greatest diameter was anteriorly in the body but some way behind the head; here the proglottids are broader than long. The scolex as a rule appears to be a little less in diameter than the ensuing region of the strobila. But occasionally, as depicted in text-fig. 1 A, the scolex stands out as a globular body followed by a constriction. In an examination of the living worms I noted one example in which there was no neck, an unsegmented region following upon the scolex; and I have one mounted preparation (represented in text-fig. 2), where the same feature is to be seen. But I have no note as to whether these examples were the same. As a general

rule there is no neck and segmentation begins immediately after the scolex. The scolex is rather small and the suckers are large in proportion, occupying most of the area of the scolex. There was no trace of any hooks whether related to a rostellum or upon the suckers. I ascertained this by transverse and longitudinal sections as well as by the examination of entire scolices mounted





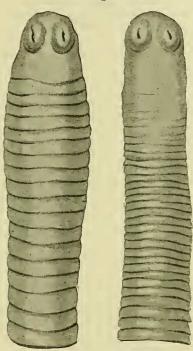
A. Head-end of an example of Rhabdometra cylindrica.

B. Another and complete specimen of the same species.

in glycerine. It is very important to be positive upon this point, since the difference between the genera *Rhabdometra* and *Paruterina* is practically entirely to be found in the absence in one and the presence in the other of a rostellum armed with hooks. The strobila consists of proglottids, which are at first narrow and then

rather wider. The end of the body, often more than one half of the entire worm, is made up of very long proglottids which I found to measure as much as five and six millimetres in length. They are thus quite as much as or even more than six times as long as they are broad. There is no one of the known species of *Rhabdometra* in which the ripe proglottids are so long as in the species described in the present communication. It may be,





Anterior end of two specimens of Rhabdometra cylindrica.

The right-hand figure shows the existence of an unsegmented neck rare in the species.

however, that the individuals of the various species examined by my predecessors were not so fully mature as those which I have myself been able to study. The greatest length of the hinder proglottids is to be found, as it would appear, in *Rhabdometra nigropunctata*, where, according to Crety*, they are three times the length of their diameter. That is considerably less than I have

^{*} Boll. Mus. Torino, v. 1890, No. 88. It should also be noted that this species which measures 140 mm., is nearest in length to mine.

met with. The anterior relatively broader segments are rather flattened in transverse section. The posterior proglottids are sometimes quite cylindrical in form, being circular in section. Or they may be more oval, though still of great depth dorso-

ventrally.

In transverse sections such as are represented in text-fig. 6, the cortical layer is seen to be fully as thick as, and occasionally even a shade thicker than, the medulla. The distribution of the longitudinal muscular layer seems to be very much as it has been described by Fuhrmann* for the allied species Rh. numida. Next to the transverse muscles there is a layer of rather widely spaced bundles with not more and sometimes less than 5 or 6 fibres in each. Between these and the subcuticular layer are numerous scattered longitudinal fibres implanted singly. The transverse fibres form a rather thick layer, and in the anterior region of the proglottid, where the medulla is free from the testes etc., and in the area partially occupied by the paruterine organ, the transverse fibres encroach further upon the medullary parenchyma, which is largely pervaded by them. Dorso-ventral fibres are also abundant in the medullary layer and, as mentioned later, are not at first displaced by the paruterine organ.

The water-rascular system consists of the two usual longitudinal vessels, of which the very much larger ventral vessels are united by an equally wide transverse vessel at the posterior end of each proglottid. The opening of the longitudinal vessel into the transverse vessel is guarded by a valve which prevents the reflux of fluid into the longitudinal vessel anteriorly. I could find no other branches of the ventral vessel to form a network such as appears to exist according to Ransom in Rhabdometra nullicollis. The dorsal vessel lies above the ventral and often rather to the inside; it is very small but has relatively thick walls. The genital ducts pass between the two vessels and below the nervecord, which is displaced towards the dorsal side from its usual position, where the ducts pass beneath it. It will be noted that in the relations of the nerve-cord to the genital ducts the present species differs from both Rh. nullicollis and Rh. similis, where

the genital ducts pass dorsal of the nerve-cord.

The testes are numerous, and often very closely pressed together. They lie on all sides of the ovary and vitelline gland, being found laterally and posteriorly as well as anteriorly in the segment. In the most mature segments the testes are only plainly to be recognised posteriorly in the segment lying behind the uterus. Laterally the testes in the ripe but not fully mature proglottids extend as far as the water-vessels on each side. Anteriorly the boundary of the area occupied by the testes is some way short of the anterior margin of the proglottid. In transverse sections of proglottids where the uterus is nearly fully developed, the testes are seen to lie dorsally of the uterus, which latter organ

^{*} Res. Swed. Zool. Exp. Egypt, pt. iii. No. 27, 1909.

occupies the whole ventral surface of the proglottid. The extension of the testes anteriorly in the segment seems to be prevented by the paruterine organ, which in those proglottids where the testes are fully ripe extends backwards for about half the length of the proglottid and takes up the greater part of the available space. It is important to insist upon the fact that the testes surround the female gonads, since this does not appear to be the case with other species of this genus *Rhabdometra* as figured by Ransom. The genus is, in fact, partly defined by the existence of the testes only behind and at the sides of the female organs. The testes are only two deep in a given segment.

The cirrus-sac is long and slender, longer than that of the species figured by Ransom, but considerably shorter than the cirrus-sac of Rh. numida of Fuhrmann, which reaches to the middle of the segment. In segments where the gonads are ripe but in which there is as yet no uterus, the cirrus-sac very nearly reaches the middle of the segment; but in older and wider segments it only just crosses the ventral water-vessel. Its course is obliquely forward from the point of opening on to the exterior, which is rather behind the middle line of the proglottid. There can hardly be said to be a genital cloaca: a funnel-shaped depression of the body, into the bottom of which the genital ducts open (the male duct anterior to the female), not showing the characters of a distinct chamber such as that of, for example, Eugonodeum. In horizontal sections the cirrus-sac often has a serpentiform outline, being like an elongated S. Occasionally it is slightly dilated at the internal end, but the cirrus-sac of this Rhabdometra never has the bottle-like form of that of many other tapeworms. consequence of its length and slenderness the cirrus is not much coiled within it, lying mostly straight or rather in an undulating line. I could detect no spines upon the cirrus when protruded. I did not observe any autocopulation. The walls of the cirrussac are thick and very muscular. The internal coat is of circularly running fibres, the outer layer fibres run longitudinally. From the internal end of the cirrus a retractor muscle runs for some way into the medullary tissue. This character is also found in other species of the genus Rhabdometra. The vas deferens forms a large coil which is situated posteriorly to the paruterine organ, and extends backward in the proglottid to as far as the receptaculum seminis. At about this point the efferent tubules from the testes meet it. There is no vesicula seminalis.

The ovary lies at about the middle of the segment. It is in

front of and larger than the vitelline gland:

The vagina is long and thick-walled, and outside of the muscular walls is a layer of stalked glands which are deeply stained by hematoxylin. The course of the vagina is directed parallel to and slightly away from the cirrus-sac to begin with; it then curves more backwards to open into the receptaculum seminis. Its course is apt to be rather undulating. Ransom has figured a sudden change in the character of the vagina in the species

described by himself, occurring at some distance from the opening into the receptaculum. It here becomes much narrower. Nothing of the kind occurs in *Rhabdometra cylindrica*, except, perhaps, just at the orifice; and, moreover, the coating of gland-cells extends over the entire vagina, up to the receptaculum. The latter is large and spherical to rather oval in form; it lies obliquely to the longitudinal axis of the body towards the pore side.

§ The Paruterine Organ.

This structure is of such importance in the group of tapeworms of which the present species is a member, that it needs a detailed treatment for comparative purposes. In the living worm the paruterine organ is exceedingly conspicuous as a rod-like body at the anterior end of the proglottid, often of a brilliant white, thus contrasting with the more pellucid tissues of the outer layers of the worm. This aspect led me at first to regard the paruterine organ as the uterus crammed with eggs, which might be expected to show a bright white owing to the innumerable separate and minute embryos. In the proglottids the increasing length of the paruterine organ could readily be observed owing to its extreme conspicuousness. It was so distinct from the rest of the proglottid in its neighbourhood, that each paruterine organ suggested a conical peg attaching two consecutive segments. In the living worms the paruterine organ is a perfectly rod-like structure, without any obvious twist of any kind. It was seen to diminish slightly in width at its terminal end, and was never seen to extend to the posterior end, though the organ appeared to commence at the very beginning of the proglottid. The whole appearance of the organ as seen with a lens, suggests that it is produced by a growth from before backwards, and not vice versa.

In alcohol-preserved examples the paruterine organ is no longer visible in the intact worm, nor is it in specimens examined whole after clearing but without staining. This seems to suggest that the bright white appearance of the paruterine organ in the living worm is caused by air-spaces in the spongy tissue of which the organ is composed. But it must be admitted that this of itself is difficult to understand. Still, the organ certainly has the appearance during life of being composed of a fine froth. I have examined the organ in the preserved worms by means of transverse and longitudinal sections. I have already spoken of the organ when fully developed as being rod-like, or perhaps rather style-like, as it diminishes to one end. But in transverse sections it is seen that the paruterine organ is only rod-like, and thus eircular in section, in the fully mature pro-These proglottids are themselves tubular and oval, or even quite circular in transverse section. In more anterior segments the form of the proglottid is more flattened, and the paruterine organ shares in this alteration of form. In such proglottids the organ is more flattened and tends to have the

shape, in transverse sections, of a parallelogram with rounded angles. The most important point in the development of this organ is that it is wholly unconnected with the uterus. The paruterine organ is found in proglottids where there is as yet no trace of a uterus.

There can, therefore, be no comparison with the paruterine organ of such a form as Avitellina, "where the uterine wall cells supply the origin of the egg-pouches or paruterine organ"*. With reference to species of Rhabdometra, the statements of Ransom are not definite. In the case of Rh. nullicollis, that author writes that "the parenchyma in front of the uterus becomes dense and fibrous and develops into a prominent paruterine organ, which behind is in immediate relation with the anterior end of the uterus." Of the paruterine organ of Rh. similis the writes no more positively. We may infer from Mr. Ransom's descriptions that the paruterine organ does not appear before the uterus and that it may be an outgrowth of its anterior wall. In this case there is an important difference from the species described in the present paper, and in any case there is a difference in time of appearance.

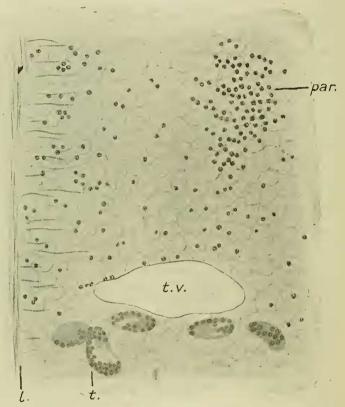
The earliest appearance of the paruterine organ under a high magnification is shown in text-fig. 3. It consists mainly in an apparent multiplication of the nuclei of the medullary parenchyma. In any case they are more closely aggregated for a short region in the middle of the anterior half of the proglottid. This dense mass of nuclei—that is dense comparatively speaking—reaches forward to the anterior border of the proglottid. But it must be borne in mind that the actual delimitation of successive proglettids cannot be fixed unless the wall of the transverse water-vascular tube fixes it. In this case the paruterine organ does not reach the anterior limit of the proglottid in which it lies. In more mature proglottids, however, the anterior margin of the paruterine organ is so straight a line that one cannot help thinking that this may be the anterior margin of the proglottid, in which case the posterior wall of the transverse water-vessel lies within the segment in front.

I have no evidence whether the great multiplication of the numbers of the nuclei to form the beginnings of the paruterine organ is due to an actual multiplication, or to a crowding together by simultaneous migration inwards from other quarters. The nuclei of the future paruterine body show no difference from the surrounding nuclei of the medullary parenchyma. I have said that the multiplication of the nuclei is the main feature of the paruterine organ on its first appearance. The only other difference from the surrounding parenchyma is a slight opacity, which is, I am convinced, simply due to the crowding of the nuclei. The network structure of the medullary parenchyma is not at first at all altered in the future paruterine organ. The

^{*} Gough, Q. J. Mier. Sci. lvi. p. 375, 1911. † Bull. U.S. Nat. Mus. No. 69, p. 29, 1909.

area occupied by the growing paruterine organ at this stage is rather more than a quarter and less than a third of the length of the proglottid. It is interesting to note that these small dimensions apply to the completely formed paruterine organ of Rhabdometra nullicollis*.

Text-figure 3.



Portion of an anterior segment of *Rhabdometra cylindrica* in horizontal section, to show origin of paruterine body.

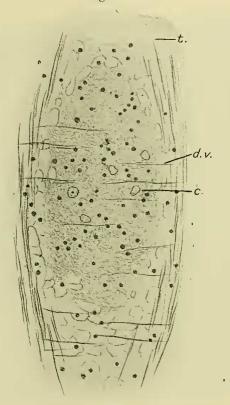
l. Longitudinal muscles. par. Paruterine organ. t. Testes. t.v. Transverse water-vascular vessel.

Text-fig. 4 illustrates a portion of a transverse section of a proglottid with a paruterine organ at a more advanced stage of development than that represented in the last figure. The paruterine organ is distinctly marked off from the surrounding

^{*} Ransom, loc. cit. p. 30, fig. 22.

medullary parenchyma in the middle of which it lies. But although it is definitely marked off, it has not an outer layer of circular muscles, such as will be described presently in the completely adult paraterine organ. The principal distinction which the paraterine organ shows in comparison with the

Text-figure 4.



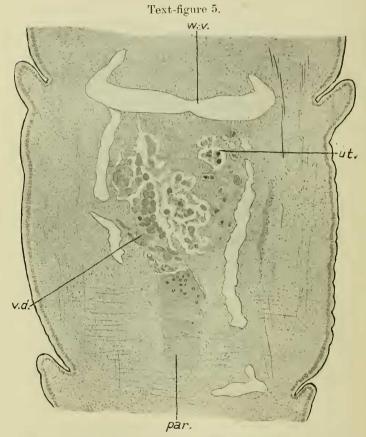
Portion of a transverse section of a young proglottid of Rhabdometra cylindrica.

The greater part of the medullary region is occupied by the paraterine organ.

c Calcareous corpuscles in the paruterine organ. d.v. Dorso-ventral muscular fibres. t. Transverse muscular fibres.

surrounding medullary region is the much denser character of the parenchyma, which no longer presents the appearance of a delicate network with clearer circular or oval interspaces. The network is here and there quite visible in parts, the whole tissue being much

more deeply stained. I take this to be due to a solidification of the tissue by the disposition of matter in the interstices of the orginally existing network, which is more responsive to staining by logwood. The nuclei are more abundant than in the surrounding medullary parenchyma. But they are in the same way

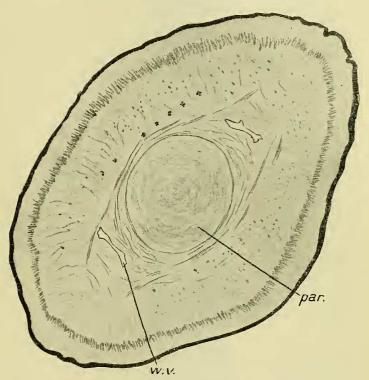


Horizontal section through not fully ripe proglottid of Rhabdometra cylindrica.

par. Paruterine organ. ut. Uterus appearing as numerous partly detached cavities. v.d. Vas deferens. w.v. Transverse water-vascular vessel.

of two kinds—larger and clearer nuclei which appear to be myoblasts, and smaller nuclei which belong to the connectivetissue network. A peculiar feature in the structure of the paruterine organ at this stage, and one which is a further proof of the view that it is a modified region of the medullary parenchyma and not an outgrowth of the generative system, is the existence of dorso-ventral muscle-fibres: these are not elements belonging to the paruterine organ and restricted to it, but, as is shown in the text-figure referred to, they arise outside of and perforate it. They pass into the paruterine organ at exactly right angles to the transverse diameter of the proglottid. A final characteristic of the paruterine organ at this stage is the



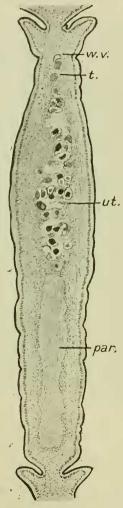


 $\label{eq:continuous} \begin{tabular}{ll} Transverse & section through fully mature proglottid of $Rhabdometra \ cylindrica$, \\ par. & Paruterine organ. & w.v. & Ventral water-vascular vessel. \\ \end{tabular}$

larger number of calcareous bodies which lie within it and which are most numerous where it abuts upon the uterus posteriorly. Ransom has remarked upon the same feature in the paruterine organ of *Sphyroncotænia*. The shape of the paruterine organ at this stage as seen in horizontal sections is shown in text-fig. 5.

In the longest, and therefore presumably ripest, proglottids the paruterine organ differs in some few particulars from its younger stages. In transverse sections, as is shown in text-fig. 6, the organ appears to be quite circular, and it lies exactly in the middle of the proglottid. It has sometimes a perfectly conical form tapering towards and at the end which touches, indeed protrudes

Text-figure 7.



Sagittal section through fully mature proglottid of Rhabdometra cylindrica.

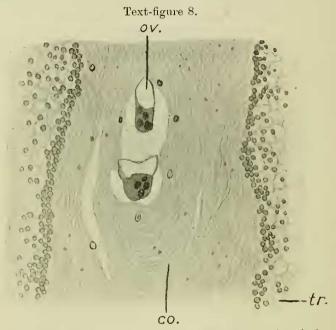
par. Paruterine organ. t. Testes. ut. Uterus. w.v. Transverse
water-vascular vessel.

into, the uterus. In other cases the diameter of the paruterine organ fluctuates from point to point, thus showing a less regular form such as is depicted in longitudinal section in text-fig. 7. This difference of form is probably to be explained by uneven contraction of the worm's body or the muscular wall of the paruterine organ during preservation. The paruterine organ is long, but not quite so long as the uterus at which it ends. It therefore occupies rather less than half of the length of the proglottid. Dorso-ventrally the paruterine organ touches the limits of the medullary region of the proglottid; but laterally it does not fill up that space entirely, leaving some of the original medullary parenchyma visible right and left. There is no question of the inclusion of any organs in the paruterine organ such as I describe later* in what appears to be the equivalent of a paruterine organ in the Davaineid genus Otiditania. completely formed paruterine organ of this species of Rhabdometra is sharply marked off from the surrounding tissues by a layer of muscles disposed in circular fashion.

The existence of such an outer muscular wall to the paruterine organ has been noted by other observers. I believe this layer to be adventitious and for the following reasons. In the younger stage just described there is no muscular wall at all; but the innermost of the transverse muscular fibres tend to follow the outline of the oval paraterine organ, though they hardly can be said to adhere to it. The contraction, or at least the alteration, of the form of the paruterine organ into a circle in transverse section would tend to further a close relationship between itself and the immediately surrounding musculature. In any case such a relationship exists. The shape in section and the general form of the paruterine organ together with its muscular coat are not, however, the only points in which the adult organ differs from the less perfected stages. The tissue which fills it is apt to have a concentric lamellar arrangement shown in text-fig. 8; this is also visible in sagittal sections but is not shown in text-fig. 7, since the latter is not of a sufficiently highly magnified preparation. It is shown, however, in text-fig. 6.

In the younger proglottids (text-fig. 5) the paruterine organ ends up in close contact with the uterus, as has been already mentioned. It ends, however, in a definite border which is a straight line. In the completely developed paruterine organ there appears to be an absolute continuity, and the connective-tissue core of the paruterine organ melts away, as it were, in the cavity of the uterus. It appeared to me that the calcareous corpuscles, which are apt to be specially abundant on the paruterine organ at its distal end though found throughout it, are both smaller in many cases and generally less abundant in the older paruterine organ. It looks as if they were used up perhaps by the growing embryos. Furthermore, the "perforating" dorso-

ventral muscles, to which I have referred in the younger paruterine organ, are in places, but by no means always, visible in the adult, as may be seen by a comparison of the figures given. They are perhaps broken by the swelling of the organ to a circular form in section, for I have seen short fibres imbedded in the connective-tissue core.



More highly magnified view of a portion of the paruterine organ in sagittal section.

co. Tissue of paraterine organ with calcareous bodies. ov. Ripe eggs contained in a space within the paraterine organ. tr. Transverse muscles.

In describing the paruterine organ of Chapmania tapika, Prof. Fuhrmann* remarks that in that and all-forms with a paruterine organ the ripe eggs do not pass into the paruterine organ until the proglottids are detached and thus ready to leave the body. Mr. Ransom† particularly remarks that in his examples of the genus Sphyroncotænia the mature segments showed no eggs within the paruterine organ and that the mode of their transference was thus unknown to him. This state of affairs is nearly true also of the Rhabdometra which forms the subject of the present communication, but not quite. In one ripe proglottid among many which I studied, I found embryos within the

† Proc. U.S. Nat. Mus. vol xl. p. 637, 1911.

^{*} Res. Swed. Zool. Exp. Egypt, pt. iii. No. 27, p. 19, 1909.

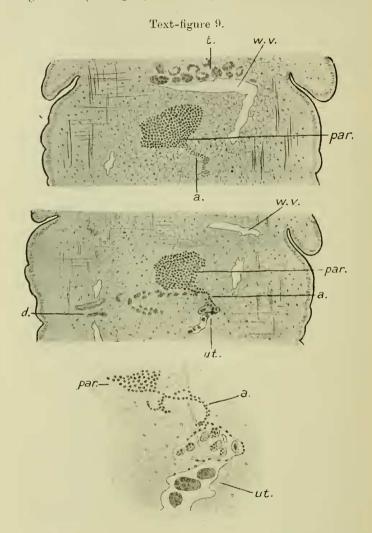
paruterine organ, thus incidentally proving that the organ is a paruterine organ, if any doubt could be supposed to attach to that identification of it. The embryos were not directly imbedded in the lax tissue of the paruterine organ but were accompanied by a cavity within which they lay. Whether this means that their assumption into the paruterine organ resulted in the formation of a cavity by stretching or other means, or whether a portion of the uterus was detached as a whole and engulfed by the paruterine organ, I do not know.

§ The Uterus.

Although the appearance of the paruterine organ before the uterns is developed proves that the former is not a product of the latter, it does not follow that there is no connection at all between these two organs in their origin. I believe that I have been able to establish a connection between the two, and that the tissue of the paruterine organ gives rise to the uterus. I am not sure that I have detected the uterus in the very first segment in which it is developed, but if not, I am not more than three or possibly four segments out. As is often the case with tapeworms. the uterus appears rather suddenly and in an advanced stage of development, at least speaking relatively. In the segment in question, which is the second or third with a uterus, the testes are still active and the ovary and vitelline glands in full maturity and not beginning to degenerate. The paruterine organ is considerably younger than that represented in text-fig. 5; in the sections (which were nearly accurately horizontal) the outline of the paruterine organ was nearly square, the breadth being a little greater than the length. The uterus consists of an irregular tube running rather obliquely across the long axis of the body. tube branches somewhat and there are indications of anastomoses: but the retiform stage of the uterus has hardly been reached. The uterus does not extend, as it does later, in front of the transversely running coil of the vas deferens. It does not. therefore, come into contact with the broad posterior end of the paruterine organ as it does in later stages (cf. text-fig. 5). There is, however, a connection between the two which is more than mere juxtaposition and is, therefore, of an interesting nature. A process extends backwards from that posterior corner of the paraterine organ which is furthest away from the pore side of the segment. It consists, like the paruterine organ at this stage, of little more than an agglomeration of nuclei. This process extends backwards until it reaches the uterus with whose walls it is continuous.

In an earlier stage, about three segments in front of that just described, a uterus can hardly be said to exist. I detected, however, a thread of paruterine tissue extending towards the same side of the body; this came into close relations with one or two spaces containing ripe ova situated in front of the uterus,

and perhaps to be looked upon as the first appearance of a uterus. I figure also (text-fig. 9) from a segment which is the one in



Upper figures represent two horizontal sections through immature proglottids of $Rhabdometra\ cylindrica$.

Lower figure a more highly magnified view of the connection between the paruterine organ (par.) and the uterus (ut.).

a. Process of paruterine organ connecting it with uterus. d. Dorsal vessel. w.v. Transverse water-vascular vessel. t. Testes. front of that first of all treated of in the present account of the development of the uterus of *Rhabdometra*. Here the connection of the paruterine organ with the uterus happens to be plainly visible in one section, and, therefore, to be more striking and less liable to doubt than when it has to be followed out from section to section. Furthermore, in subsequent sections, where the uterus is more advanced and lies also in front of the vas deferens, the tissue of the paruterine organ is seen to pass continuously into that of the uterus, and the nuclei of the walls of both appear to be identical.

These facts—that is to say if it be agreed that they prove a connection between the paruterine organ and the uterus—enable us to get over certain morphological difficulties relating to the homologies of the uterus and paruterine organs of some other

Tapeworms.

In describing the structure of *Inermicapsifer capensis** I had to refer to an important difference in the uterus of this form as compared with other species referred by v. Janicki† to that genus (his own). Briefly put, the difference is this: in *I. capensis* there was no continuous uterus, but only a series of detached cavities which appeared to be formed independently in the medullary parenchyma. These cavities were formed subsequently to the extrusion of the ova from the ovary and their scattering through the parenchyma of the medulla. Furthermore, there was also to be observed, and again unconnected with the ova at first, a condensation of the medullary nuclei to form a kind of network pervading the medulla. This network was often to be observed in relation to the ova ‡.

Out of this dense tissue, which ultimately surrounds the ova, is formed the series of paruterine organs which characterise this, as well as a few other genera of tapeworms (Davainea, Thysanotænia). I held that the network of parenchymal tissue, out of which the paruterine organs were formed, and the cavities in which lay the eggs singly or in groups, were not the equivalents of the branched uterus described by v. Janicki in an allied form, Inermicapsifer hyracis (which I removed to the genus Zschokkeella), because, if it were, it would be a subsequent stage due to the obliteration of the pre-existing cavity; and as the ova appeared in it later it could not be a subsequent stage. I believe that the matter becomes clear through the observations which I have recorded in the present paper. We have in Rhabdometra, as in Inermicapsifer, a condensation of nuclei to form structures or cavities to contain the eggs. In Rhabdometra there is one extensive condensation of the kind to form the paruterine organ and a delicate strand which extends through part of the rest of the medullary parenchyma and would appear to be the seat of the formation of the uterus. In my species of *Inermicapsifer* there is the same condensation of the

^{*} P. Z. S. 1912, p. 588, etc.

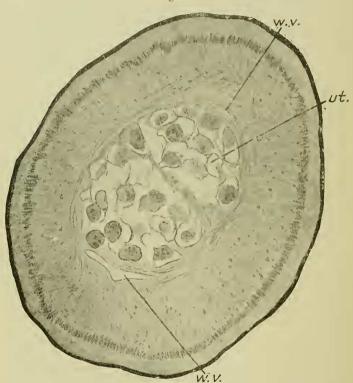
[†] Jen. Denkschr. xvi. 1910. ‡ Beddard, loc. cit. text-fig. 67, p. 588.

medullary parenchyma, but it does not become much hollowed out to form a uterus or specially condensed in one part to form a

single paruterine organ.

On the contrary, it is condensed here and there to form several paruterine organs. In *Inermicapsifer hyracis* of v. Janicki, a hollowing out of the strands of condensed tissue occurs before the further condensation of the medullary tissue to form the numerous paruterine organs. I am of opinion that all these rather various





Transverse section through mature proglottid of Rhabdometra cylindrica.

ut. Uterus. v.v. Lateral water-vascular tubes.

cases are upon one common ground plan, which does away with the at first apparent differences of importance between such closely allied forms as *Inermicapsifer capensis* and *Zschokkeella* hyracis; and also relegates to the same category other forms in which there is but a single paruterine organ. If these suggestions thus briefly sketched out be not accepted, there still remain the

facts which I have described above in connection with the formation of the uterus in Rhabdometra cylindrica. I have mentioned that the uterus soon after its formation is distinctly retiform, the network being irregular but very plainly to be seen in horizontal sections. In transverse sections, the uterus is seen to lie ventrally and to consist of variously sized cavities detached from each other, which is, of course, the expression of the horizontal network when seen in that aspect. mature proglottids the retiform condition is not so clear and the uterus occupies much more of the proglottid. The arms of the network seem to have coalesced, forming an irregularly shaped body with partial septa dividing its interior into partly detached cavities, and with outgrowths producing a general irregularity of surface. In the completely mature proglottids the appearance of the uterus has again changed owing to further development. Text-fig. 10 shows a transverse section of such a proglottid, and the contained uterus is seen to be circular in section and thus to be rod-like in form. Posteriorly the uterus is divided by a median septum into two equisized halves, but further forward the uterus is obviously single, but the interior is divided by many ingrowing strands of the medullary tissue into a series of chambers each of which is seen to lodge but a single embryo. The posterior division of the uterus into two reminds us of the uterus of Rhabdometra nigropunctata as figured by Crety*; it is possible, however, that the latter form is rather to be referred to the genus Metroliasthes, in which the uterus is an entirely double structure. The series of changes in the appearance of the uterus in this species of Rhabdometra is very remarkable, and seems to contrast with what has been observed in the other species of the genus. further to be noted that we have here, as a temporary phase, a form of uterus which is now characteristic of one genus of Tapeworms and now of another.

From the above account we can abstract the following description of the species:—

Rhabdometra cylindrica, sp. n.

Length 150 mm.; greatest diameter 1.2 mm. Scolex of less diameter than strobila following, suckers proportionately very large; rostellum and hooks absent. Neck absent; posterior segments elongated, five times their diameter, cylindrical in form. Genital apertures alternate irregularly, behind middle of proglottid. Genital ducts pass between water-vessels and ventral of nerve-cord. Cortical layer thick; longitudinal muscles not in strong bundles; mostly implanted singly, but a row next to transverse layer of widely spaced bundles with from two to five or six fibres. Circular layer

^{*} Boll. Mus. Torino, 1890. In Crety's figure the two posterior and globular diverticula of an anterior curved portion are alone represented as containing eggs. I assume, therefore, that the anterior part is all of it to be regarded as a paruterine organ.

well marked and also occupying, in the form of scattered fibres, most of the medullary layer in the region of the paruterine organ. Dorsal water-vessel very small, lying dorsal of large ventral vessel, which communicates with its fellow posteriorly in each segment by a single transverse ressel; no excretory network. Testes surround ovary and vitelline gland. Cirrus-sac with a strong muscular wall, and with special retractor muscles posteriorly, long and narrow, extending a little beyond water-vascular tubes: cirrus without spines; vas deferens with a large and close coil but without resicula seminalis. Cirrus-sac opens into a cloaca genitalis. Vagina opens behind cirrus sac, terminal region wide and muscular. Uterus at first retiform, then irregular in shape with outgrowths, later tubular and divided into two chambers by a median septum posteriorly: the embryos also separated by ingrowths of walls of uterus. Paruterine organ long and styliform, commencing at anterior end of proglottid, nearly circular in transverse section when mature, appears before uterus.

Hab. Caccabis melanocephala.

§ Systematic Position.

It is clear that a member of the Tanioidea with a totally unarmed scolex, with one set of genitalia in each proglottid, and with a single paraterine organ, can only belong to one of the three genera *Rhabdometra*, *Anonchotænia*, or *Metroliasthes*, or to

a new genus allied to them.

As it is, these three genera are very near together; the generic differences as set forth by Ransom mainly concern the position of the genital ducts with reference to the water-vessels and the form of the uterus. In both of these particulars the present species is like Rhabdometra; sufficiently so also, in other features, to warrant its inclusion in that genus. There are, however, differences which prevent the reference of my species to any of those which have been already described. In none of the hitherto described species are the segments so long as in the present form. Rhabdometra nigropunctata has the longest of any; but here the most posterior are only 3×1 .

There is, to my mind, no doubt that the species which is nearest akin to that which I here name Rhabdometra cylindrica is Fuhrmann's recently described Rh. numida*, and it will be observed that both come from the same part of the world and they both infest gallinaceous birds. There are, however, sufficient differences to warrant specific separation. Thus, Rh. numida is a small species 60–70 mm., and has not, as already mentioned, elongated posterior proglottids. Although the two species agree in possessing a long cirrus-sac, that of Rh. numida is much the longer, reaching as it does to the middle of the body. Nothing is said as to the development of

^{*} Res. Swed. Zool. Exp. Egypt, Pt. iii, No. 27, p. 36, 1909.

the uterus; but it is, when fully matured, a lobate sac, and apparently not strictly cylindrical, as in my species. On the other hand, the paruterine organ is represented as appearing first, and the course of the vas deferens is as in my species and not as in some others. Further, the genital apertures of Rh. numida are behind the middle line of the proglottid, and the testes come nearer to surrounding the ovary than in other species, except Rh. cylindrica. Finally, the generative ducts lie between the water-vessels and ventral to the nerve-cord. I have observed

the same relationship in Rh. cylindrica.

It is possible, of course, that previous authors have not seen quite fully-developed examples of the species studied by them. In view, however, of the published figures of the uterus and paruterine organ in the several species, I am inclined to doubt this. For example, Ransom's figure of that organ in Rh. similis* shows the "flowing appearance" of the core of the paruterine, which I find only in that organ when fully developed (see text-fig. 8, p. 872). As to other species, it does not appear that the reticular uterus of Rhabdometra cylindrica, a condition which precedes its cylindrical final form, has any likeness to what has been observed in previously described forms. This, indeed, coupled with the form of the paruterine organ and a number of minor points, such as the posterior position of the generative apertures, the position of the coil of the vas deferens, and the distribution of the testes, seem perhaps after all to necessitate generic separation. But this I leave for the present. It must be remembered, however, that the scolex of this species of Ransom is unknown, and that apart from this character it is hard to distinguish Rhabdometra from Paruterina.

§ A Note upon Otiditænia eupodotidis Beddard.

After communicating to the Society † my note upon this new tapeworm from Eupodotis kori, it was suggested to me that it was possibly identical with or near to a recently described new genus and species Sphyroncotænia uncinata. I had not at that time seen Mr. Ransom's paper ‡, which only (through his kindness) reached my hands after my memoir was in the press. I was, therefore, unable to make any comparisons. A consideration of the structure of this genus Sphyroncotænia, leads me to revise what I have written concerning the affinities of Otiditænia; but the two genera are not identical. In Sphyroncotænia the body is much more elongate than in Otiditænia; the genital pores are unilateral; there are many rows of minute hooks upon the rostellum, and the uterus appears to be racemose and to extend

^{*} Loc. cit. p. 35, fig. 26.

[†] P. Z. S. 1912, p. 194. ‡ Ransom, "A New Cestode from an African Bustard," Proc. U.S. Nat. Mus. xl. p. 637, 1911.

much further into the ripe proglottid than it does in Otiditania. I have re-examined my preparations of Otiditania, and find that my report upon its structure as regards the above points in which

it differs from Sphyroncotænia is correct as to fact.

But I find that I have missed one point of resemblance to Sphyroncotænia, and through it, to the subfamily Idiogeninæ of the Davaineida. This has, of course, an important bearing upon the classification and position of Otiditania in the system. While admitting its resemblances to Davainea, and by inference to the Davaineidæ, I was inclined to place Otiditania nearer to Choanotenia and its allies. This was, undoubtedly, due to my not having seen a paruterine organ, though its presumed absence was not made use of in the generic definition *, or in the résumé of the most noteworthy characters of the genus following the definition. Nor, indeed, do the nearly mature proglottids show any structure exactly resembling the paruterine organ of Idiogenes, Stilesia, Anonchotænia, Sphyroncotænia, Rhabdometra, and other forms as figured by various zoologists in memoirs known to me. In all of these instances, and in others, the paruterine organ is represented as a structure of fibrous appearance and of limited size, formed apparently from a metamorphosis of the medullary ground-tissue in the immediate neighbourhood of the uterus or from the walls of the uterus itself. This latter origin is asserted by Gough † for Avitellina centripunctata, while Ransom's figure # of a "mature segment becoming gravid" of Rhabdometra similis may be interpreted in a like manner. But whatever be the origin of these paruterine organs §-and both Fuhrmann and Gough believe them to be not strictly homologous through the series-they would appear to have been described as small bodies lying in, and possibly derived from, but ultimately independent of, the medullary parenchyma.

In Otiditania, however, the more mature segments show an alteration in the medullary parenchyma to which I have referred, and which I have figured in my memoir upon that genus |. This alteration affects the whole of the medullary parenchyma as seen in that section \(\) of a nearly mature proglottid. It is visible up to the circular muscular layer which forms the line of demarcation between the cortex and the medulla, except where it is separated therefrom by the ventral water-vascular tube as is also shown in my figure. The dorsal smaller water-vascular vessel lies well within the core of medullary parenchyma, as is also shown in the figure referred to. There is not, therefore, to be

^{*} Loc. cit. p. 220.

^{† &}quot;A Monograph of the Tape-Worms of the Subfamily Avitellining." Quart. Journ. Micr. Sci. Ivi. pt. 2, 1911, p. 375.

‡ "The Tænioid Cestodes of N. American Birds." Bull. U.S. Nat. Mus. No. 69,

^{1909,} fig. 23, p. 31.

[§] I do not refer here to the multiple paruterine organs of Davainea, Zschokkeella,

Loc. cit. p. 218, text-figs. 23, 24, 26, 29. Loc. cit. fig. 29, p. 212.

observed the formation out of the medullary parenchyma of a definite structure that can be called a separate organ, since the modified region of the proglottid extends over the whole medullary

parenchyma and includes the dorsal vascular tube.

I have also figured in my paper referred to stages which are anterior to that which has just been redescribed. In text-fig. 26 of the paper referred to*, three proglottids somewhat younger are represented in sagittal section. A glance at this figure might convey the suggestion that a definite paruterine organ of limited extent lay in each of these proglottids, narrower at one end (where the letter "T" in the diagram is placed) and wider at the other. Furthermore, the slightly twisted outline of the (alleged) paruterine organ recalls that of, for example, Rhabdometra nullicollis †. A more careful scrutiny of these sections, however, brings to light the following facts which are of importance in the matter. Although, as depicted in my illustration, the edge of the (alleged) paruterine organ is apt to be wavy and thus to create inequalities in its diameter, suggestive of a solid body of irregularly curved outline, it will be found that the waviness is closely followed by the layer of transverse musculature which separates, in this as in other tapeworms, the cortical and medullary layers. Unequal contraction during preservation is, as I think, responsible for this undulating disposition of the line of transverse muscular fibres. The object, however, of my figures referred to was not to show the structure of the medullary parenchyma but to indicate the position and relations of the uterus. The minute structure of the medullary region in this stage is less modified than that of the older proglottids already referred to. The medullary groundwork is traversed by numerous rather stout muscular fibres, running mainly if not entirely in a dorso-ventral These are very frequent, but are single and not aggregated into bundles excepting at the anterior end of the proglottid; here the testes of this segment in front are separated by a thicker layer of these muscles from the parenchyma of the ensuing segment, the groundwork is comparatively dense, and there are abundant nuclei. I have recognised that in those proglottids, as well as in the more mature ones, the dorsal watervessels are included in the medullary tissue. In comparing this stage with the older one that has just been described, it appears that the latter differs only in the degeneration of the muscular fibres of the ground-tissue, which produces the more fibrous and, at the same time, laxer appearance of the medullary parenchyma, which, however, may be more resistant, and which is still further exaggerated in the distended perfectly ripe and detachable proglottids at the end of the worm's body. This laxity favours the movement into the interior of the embryos from the uterus, which I have described in my paper as occurring in

^{*} P. 204

[†] Ransom, Bull. U.S. Nat. Mus. No. 69, p. 29, fig. 21, 1909.

these proglottids. It should, furthermore, be noticed that while the medullary tissue is, as already stated, separated anteriorly from the testes, there is no such separation posteriorly where it abuts upon the uterus, nor is the epithelial lining of the latter apparent in these older proglottids; thus the transference of the eggs into the medullary parenchyma is rendered easier. Finally, I have observed that the calcareous corpuscles tend to accumulate more thickly where the medullary parenchyma touches the uterus, though they are also present elsewhere and in some numbers here and there.

To compare with the above older stages in the growth of the sheltering apparatus for the developing embryos, I have again studied younger stages such as is represented in text-fig. 25 of my paper referred to *. I have, however, more especially studied sagittal sections, as in the case of the older proglottids. In such sections there should be visible the origin of the paruterine body, were this structure in the genus Otiditenia of the same nature as that of Rhabdometra, etc. But I can find no trace of any particular condensation and fibrillation of a definite region of the medullary parenchyma which might later spread and involve the whole region, which is thus involved in mature proglottids, but for other reasons.

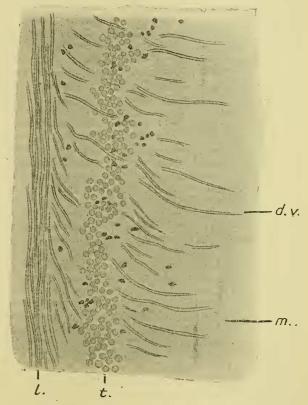
Not only is there nothing of this kind to be observed in the less mature proglottids, but there is no approach towards the fibrous appearance of the mature proglottids. This latter appearance is, in fact, produced by a new growth, which seems to be very remarkable. I have already referred in my account of the proglottids of intermediate age to abundant dorso-ventral muscular fibres in the medulla; it is, perhaps, to the unequal contraction of these by the preservative reagent that the irregular outline of the medullary parenchyma is due, which I have commented upon as simulating a paruterine organ of limited extent, lying in the medullary parenchyma. I now call attention again, in a more particular way, to these muscle-fibres. In his account of tapeworms of the subfamily Avitellinine (of the family Anoplocephalidæ), Gough † enters in some detail into the histology of Avitellina centripunctata, including that of the muscular system, which I may conveniently take as a basis of comparison with Otiditania, which shows an important difference. Gough points out that the dorso-ventral muscles which traverse the medullary parenchyma in that direction, consist mainly of bipolar myoblasts with terminal fibrillæ and, to a less degree, of bipolar myoblasts with lateral fibrilla. The larger muscular fibres, which are tubiform with an axially contained myoblast, are limited to the longitudinal muscular layer. My own observations upon various genera which I have examined confirm this generalisation. The delicate dorso-ventral muscle-fibres of such

* Loc. cit. p. 202.

[†] Quart. Journ. Micr. Sci. vol. lvi. 1911, p. 347 et seg.

tapeworms as I have known hitherto, often curled into a spiral or at least an undulating course, are excessively slender as compared with the longitudinal muscles. In *Otiditenia*, however, we meet with the very surprising state of affairs represented in the annexed figure (text-fig. 11). Imbedded in the nucleated parenchyma are numerous scattered muscular fibres, which have a general

Text-figure 11.



Sagittal section through a portion of proglottid of Otiditænia eupodotidis.

dorso-ventral direction and must be regarded as the dorso-ventral musculature. But the fibres themselves are distinctly of the character of the fibres of the longitudinal muscular layer. They are long, straight fibres of even diameter, and I traced them through the layer of circular fibres which bounds the medullary

parenchyma externally. These fibres, however, are not exactly like those which constitute the longitudinal muscular bundles. Although very wide when compared with the delicate fibrils that one expects to find in this situation, they are little if anything more than half the width of the longitudinal fibres. There is also a difference in the way in which they absorb the logwood stain, indicating a denser, because more deeply stained, outer layer. I do not attempt a further description of these fibres, as the material was not preserved in a way likely to bring out greater detail of structure. But enough is plainly visible to show that the dorso-ventral musculature in this worm is different from that usually met with in this situation among tapeworms. It is now necessary to point out that, in the younger proglottids, these thick dorso-ventral muscles are not visible. As the mode of preservation and staining has been identical, there can be no question here of a failure to detect the fibres in question, which I have looked for both in transverse and sagittal sections. Fine delicate fibrils can be seen, but nothing like the muscles just described, which are even recognisable under quite low powers. It seems clear, therefore, that they appear; but whether they do so in the shape of new fibres or of a thickening of more slender fibres present in the younger proglottids, I am unable to say. But in any case there is a change of structure in the medullary parenchyma as it grows older which is not a degeneration, and which appears, therefore, to be a preparation for some function, which is possibly that of a receptacle for the ripe embryos. It is for these reasons that I think myself justified in speaking of a paruterine organ in Otiditania which is, however, of a most generalised

The above description amounts in reality chiefly to an emphasised re-assertion of the facts concerning the medullary parenchyma of Otiditania, already dealt with in my paper on that genus. The facts lead me to the inference that we have in this tapeworm the commencement of the formation of the paruterine organ, which is more differentiated in other genera of Davaineide, as well as in the Paruterine among the Hymenolepididæ. The paruterine organ of Stilesia, and that of its immediate ally Avitellina, seems to me to be a different structure altogether, though serving much the same function. In Otiditania, then, there is an alteration of structure in the whole medullary layer in the direction of increased firmness: but there is no special part of that parenchyma set apart for the sheltering of the growing embryos. In a sense, therefore, I was right in not describing the existence of a paruterine organ; but with equal truth it may be said that this genus has the equivalent of a paruterine organ. In this genus we see the next stage to that exhibited by many genera in which the ripe embryos lie in the unaltered parenchyma, such as Oochoristica, Linstowia, etc. A. slight increase of specialisation of the conditions observable in Otiditania leads us at once to such a form as Sphyroncotania,

where a large conical paruterine organ exists which is distinct from the surrounding medullary parenchyma.

§ Systematic position of Otiditania.

I shall now reconsider the systematic position of Otiditænia in the light of the foregoing revision of certain facts in its anatomy.

As to the hooks which would form so important a means of preliminary family identification, I am not yet certain whether they are or are not the typical Davaineid hooks. They may well be so; but as I have not been able to view them sideways in my preparations I am unable to be positive. They may prove to be like those of Oligorchis paucitesticulatus * for example. There is, however, no doubt that this genus is not in any case a near ally of Oligorchis or Hymenolepis, so that we may perhaps fairly assume that the hooks after all conform to the idea that Otiditænia is to be referred to the Davaineidæ. Of this family Mr. Ransom has lately † made a useful table of classification which is an extension quite up to the present date of the table

in his revision of the Cyclophyllidea ‡.

From the table in question it appears that Otiditenia will come nearest to Chapmania. The matter for immediate settlement is, therefore, whether the two genera are to be regarded as identical, in which case my name will obviously have to be dropped. It must be remembered, however, that this near alliance depends upon whether we are to look upon Otiditania as possessing a paruterine organ; otherwise (still considering it for other reasons to be a Davaineid) Otiditania will be nearer to, or identical with, either Davainea or Ophryocotyle. As to Davainea, we may at once dismiss the idea of near affinity; for in that genus the ripe embryos are included in numerous separate paruterine sacs quite unlike the paruterine organs of Idiogeninæ. The knowledge of the genus Ophryocotyle mainly depends upon the descriptions of O. insignis of Lönnberg, the most recent of which is in a memoir by Fuhrmann §. This worm is to be at once distinguished from mine by the immense number of hooks, 2000, which are disposed in an undulating line round a particularly large rostellum: furthermore, the uterus, which is slightly lobate in form, lies behind the ovary, while the testes are dorsal to as well as behind the ovary. Moreover, the uterus shows no tendency to break up; it is conceivable, however, that it might later, in view of the very late breaking up of the uterus in Otiditania. Finally, Ophryocotyle is to be characterised by multiple rows of minute hooks upon a portion of the suckers. This latter character does not seem to be found in Otiditania.

^{*} Fuhrmann in "Nordische Vogel-Cestoden aus dem Museum von Göteborg," Medd. Göteborg. Mus. Zool., Afd. i. p. 18, fig. 8.

† "A New Cestode from an African Bustard," Proc. U.S. Nat. Mus. xl. 1911, p. 637.

‡ Bull. U.S. Nat. Mus. No. 69, 1909.

[&]amp; Centralbl. f. Bakt. Paras. Bd. xlix, 1909, p. 91.

But in the case of these hooks upon the suckers, it would appear that in Chapmania they tend to drop off. This difference, therefore, between Otiditænia on the one hand, and both Ophryocotyle and Chapmania on the other hand, must be held in reserve until more specimens have been examined. There is, however, I think, no doubt that Otiditania is quite distinct from Ophryocotyle, if only by reason of the characteristic rostellum of the latter. There now remains only the genus Chapmania. The first obvious point of difference between the two supposed genera is the armature of the suckers in Chapmania; but, as already admitted, we cannot apparently dwell too strongly upon this, for the reason that these hooks are said to be occasionally shed from the suckers in Chapmania. I have, however, examined the suckers in two specimens of Otiditumia; and the examination of two examples lends naturally further support to the view that the hooks are really missing. Apart from this, there are apparently two main points of difference which forbid a fusion of these genera. In Chapmania tapika—which species alone comes into comparison with Otiditania, for Ch. taurika has unilateral generative pores and in other respects differs perhaps to a generic extent from its supposed congener—a tentacle arises from each sucker; this is figured by Furhmann as elongated and conical. I have found nothing of the kind in longitudinal and transverse sections of the scolex of Otiditania. It may be urged that this failure to discover a similarity may be due to the complete retraction of the sucker tentacle, and thus to the difficulty of detecting This may be so; but in the meantime I have seen, in a tapeworm from Numida (which may perhaps be the very species, Chapmania tapika), the tentacle freely moving about in the living worm. Having thus recognised the structure, it is of course less likely that I should miss it in examples where it was carefully looked for. Besides, the apparent non-retraction of this tentacle in the preserved examples of Chapmania examined by Fuhrmann, leads to the inference that it would be present in an unretracted condition in my spirit-preserved specimens of Otiditania, were it a character of that species. The next point of difference is the paruterine organ. If we are to regard the modified medullary parenchyma in its entirety as the paruterine organ in Otiditania, the corresponding organ of Chapmania as figured by Clerc * is distinctly different.

Neither Fuhrmann nor Clerc gives much in the way of description of the organ. Judging from the figure the paruterine organ of *Chapmania* only occupies about half of the ripe proglottid. It extends towards the uterus, which occupies about the other half, and ends on its side turned towards the uterus in a flat surface. This is obviously totally different from the structure which I have figured in *Otiditænia*, and considered to be possibly a paruterine organ. On the other hand, the breadth of the

^{*} Centralbl, f. Bakt, u. Paras, Bd, xlii, 1906, p. 722.

paruterine organ in Chapmania lends some support to a comparison; for it is as wide as the medullary parenchyma, which it entirely fills anteriorly, thus contrasting with the much narrower paruterine organ as figured in *Idiogenes*. I should also add that the supposed paruterine organ of Otiditania has no line of demarcation from the uterus such as is figured by Clerc in Chapmania. As points of minor importance, the uterus is lobate in Chapmania and ends much further forward in the segment than it does in Otiditania. The ripe and detached proglottid figured by Fuhrmann * is apparently not unlike that of Otiditænia. But it may be seen that the paruterine organ is more or less completely filled with the ripe embryos, whereas in Otiditænia as I have mentioned, the ripe embryos are not scattered throughout the whole of the supposed paruterine organ.

The testes of Chapmania are described as being dorsal, whereas in Otiditænia they are posterior, and no more dorsal than ventral. Concerning the muscular system of the genus Chapmania, there is a difference of opinion between Fuhrmann and Clerc. The latter regards it as feebly developed, the former as strong; in the latter event Otiditænia agrees with Chapmania. One would like to know something of the genera Ascometra and Schistometra of Cholodkovsky, which are to me at present merely names, being included in a Russian catalogue of parasitic worms †. As these genera occur in Bustards they are quite possibly Davaineids. I do not attempt to redefine Otiditænia until I learn whether it be held by others that the paruterine organ described above is a structure referable to that category, and therefore of great importance as a generic character among the Davaineidæ, to which family I now distinctly refer Otiditænia.

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^{*} Res. Swed. Zool. Exp. Egypt, Pt. iii. No. 27, p. 22, fig. 16, 1909. † Cf. Zool. Rec. 1912.